Early evolution of Cupedidae revealed by a mid-Cretaceous reticulated beetle from Myanmar (Coleoptera: Archostemata)

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Abstract.

Cupedidae, the most species-rich family of the archaic suborder Archostemata, were abundant, diverse and widespread in the Mesozoic, yet little is known about the early evolution and biogeography. This stems, in part, from a lack of exceptionally preserved fossils from the Mesozoic and of formal phylogenetic study of

both extant and extinct taxa. Here we describe and illustrate a new fossil from mid-Cretaceous Burmese amber, and provide a phylogeny combining both fossils and all known extant genera of Archostemata. A dataset of 43 in-group taxa and 4 out-group taxa based on 110 morphological characters was analyzed under parsimony. The results indicate that *Priacma* LeConte and *Paracupes* Kolbe, as well as the Cretaceous genera *Barbaticupes* Jarzembowski *et al.* and *Mallecupes* Jarzembowski *et al.*, together form a sister clade to the rest of Cupedidae. *Priacma megapuncta* **sp.n.** is attributed to the relict North American *Priacma* by the presence of distinct subtruncate elytral apices, lateral elytral margins with two rows of sharp teeth, and peculiar fixing epipleural folds near the elytral apices. Our discovery of the first fossil species of *Priacma* in Burmese amber reveals the antiquity and wider distribution of the genus in the late Mesozoic.

Introduction

The beetle suborder Archostemata is currently a comparatively small group of Coleoptera, with 45 species occurring in South America, North America, Europe, Asia, and Australia (Hörnschemeyer, 2016). Compared to their extant fauna, archostematans were abundant and diverse in the fossil record, especially from the Mesozoic era (Hörnschemeyer, 2016; Kirejtshuk *et al*., 2016). The earliest-known beetles from the Permian are superficially like Archostemata (Ponomarenko 1969), but represent stem-group Coleoptera (Beutel & Friedrich, 2008; Hörnschemeyer, 2016). Archostemata currently comprises Cupedidae, Ommatidae, Micromalthidae, Crowsoniellidae, and possibly Jurodidae (Hörnschemeyer, 2016), but the interrelationships among them remain unsettled, as phylogenies based on morphological characters and molecular data have yielded inconsistent topologies (e.g., Beutel *et al.*, 2008; Hörnschemeyer, 2009; Lawrence *et al*., 2011; McKenna *et al.*, 2015; Linard *et al.*, 2018). It is noteworthy that some authors adopted a broader concept of Cupedidae, regarding the family Ommatidae as a subfamily within Cupedidae *sensu lato* (e.g., Ponomarenko, 2000; Kirejtshuk *et al*., 2016).

Among extant archostematan families, Cupedidae (or reticulated beetles), characterized by a widened subapical tarsomere and capitate galea, is the most species-rich group with thirty-one extant species attributed in nine genera (Hörnschemeyer, 2009; Hörnschemeyer & Yavorskaya, 2016). A comprehensive morphology-based phylogenetic analysis by Hörnschemeyer (2009) indicated that the species-poor genera *Priacma* LeConte and *Paracupes* Kolbe together comprise the sister clade to the rest of crown-group

Cupedidae. Although Cupedidae is the most diverse archostematan family today, fossils belonging to Cupedidae appear to be much more abundant and diverse in the Mesozoic than in the present (Kirejtshuk *et al*., 2016). Fossil cupedids are mainly preserved as compressions, of which many key characters are usually not well preserved or simply missing, obscuring reliable interpretation. Mesozoic cupedids are of great significant for understanding the origin and early diversification of this family, but the systematic positions of Mesozoic cupedids have never been tested in a formal phylogenetic analysis (e.g., Tan & Ren, 2009; Kirejtshuk *et al*., 2016). This stems, in part, from insufficient preservation of morphological features in the previously described compression fossils. Unlike compression fossils, amber, or fossilized resin, can preserve astonishingly fine details of bioinclusions with high fidelity. The mid-Cretaceous Burmese amber deposit in northern Myanmar is one of the most prolific and extensively studied sources of Mesozoic exceptional faunas (e.g., Grimaldi *et al.*, 2002; Shi *et al*., 2012; Cai *et al*., 2017; Cai *et al.*, 2018; Xing *et al.*, 2018). Recent years have witnessed exciting discoveries of an increasing number of archostematan beetles from this mid-Cretaceous Burmese amber. Most described archostematans are represented by members of the extant Southern Hemisphere family Ommatidae (Jarzembowski *et al.*, 2016, 2017a, 2017b, 2018a, 2018b; Jarzembowski & Wang, 2016; Liu *et al.*, 2017; Yamamoto, 2017). By contrast, only three species, *Barbaticupes combertiae* Jarzembowski *et al*., 2017c, *Mallecupes qingqingae* Jarzembowski *et al*., 2017d and *M. cleevelyi* Jarzembowski *et al.*, 2017e, have been assigned to the family Cupedidae *sensu stricto* (= Cupedinae *sensu* Kirejtshuk *et al*., 2016). Based on our observation of more than 23,000 pieces of fossiliferous Burmese amber in our collection, cupedids appear to be rather rare when compared to other common archostematan species that can be placed in extant *Omma* Newman (Ommatidae). Here we report on the discovery of a novel cupedid species from Burmese amber. This fossil can be placed in the extant genus *Priacma* (Fig. 1), and provides insights into the early evolution of Cupedidae.

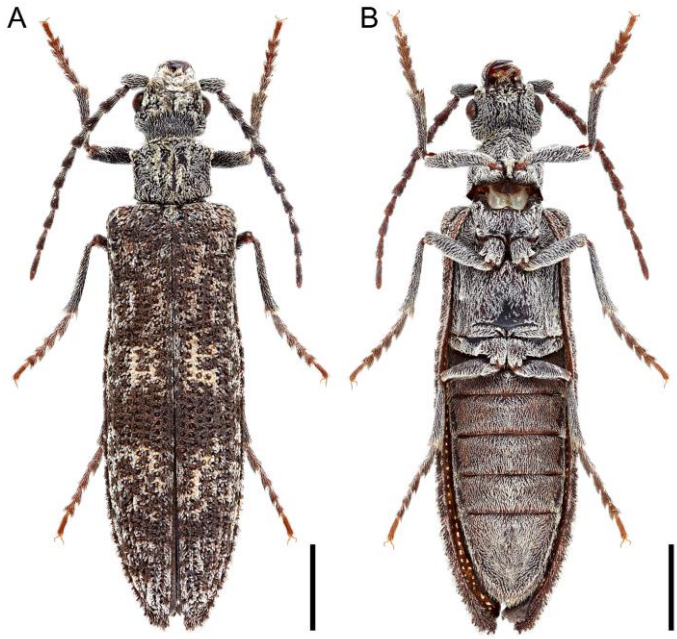

Fig. 1. *Priacma serrata*, the sole extant representative of *Priacma* from North America. Scale bars, 2 mm.

Material and methods

Material and photography

The Burmese amber specimen containing the new species studied here is derived from the Hukawng Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar. The holotype (NIGP168831) is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery papers of different grain sizes, and finally polished with polishing powder. The holotype is a nearly completely preserved adult, with almost all morphological details visible, but the apical six antennomeres of the right antenna were polished away. Three previously published cupedid species were also re-examined, including *Barbaticupes combertiae* (NIGP166314 & NIGP166315, Fig. S1), *Mallecupes qingqingae* (NIGP157008 & NIGP164791, Fig. S2) and *M. cleevelyi* (NIGP164792, Fig. S3).

Observations and photographs were taken under incident light using a camera-attached to a Zeiss Discovery V20 stereo microscope, a Leica M205 C stereo microscope and a Canon EOS-1D X camera with a Canon MP-E 65mm f/2.8 1–5x macro lens. Epifluorescence images were obtained with Zeiss Axio Imager 2 light microscope combined with fluorescence imaging systems. Images were stacked with CombineZP,

Helicon Focus 6 and Adobe Photoshop CC. The morphological terminology follows Hörnschemeyer (2009) and Hörnschemeyer & Yavorskaya (2016). The measurements were taken as follows: body length from apex of mandible to elytral apex; head length from mandibular apex to anterior margin of pronotum (from dorsal view); head width as maximum width of head across eyes; pronotal length as maximum length of pronotum; pronotum width as maximum width of pronotum; elytral length from anterior margin to apex; elytral width as maximum width of each elytron.

Taxa sampling, characters and phylogenetic analyses

Taxon selection was mainly derived from a previously published work by Hörnschemeyer (2009). Exemplars included: (i) four outgroup taxa: *Blattella germanica* (Linnaeus) (Blattodea), *Sialis lutaria* (Linnaeus) (Megaloptera: Sialidae), *Trachypachus* sp. (Adephaga: Trachypachidae) and *Elateroides dermestoides* (Linnaeus) (Polyphaga: Lymexylidae); (ii) a total of 39 extant species of all extant genera of the families Cupedidae, Ommatidae, Micromalthidae and Crowsoniellidae; and (iii) four mid-Cretaceous cupedids from Burmese amber, including *B. combertiae*, *M. cleevelyi*, *M. qingqingae* and *P. megapuncta* **sp.n.**

The morphological data matrix was mainly modified from the dataset for extant archostematan phylogeny (Hörnschemeyer, 2009). We removed the enigmatic species, *Sikhotealinia zhiltzovae* Lafer, from the data matrix, because its subordinal placement remains contentious (Yan *et al.*, 2014, and references therein). An obscure and poorly defined character (median protuberances, character #14 in Hörnschemeyer, 2009) was removed in our analyses. Specifically, the description of median protuberances (P3) on the head of some extant cupedids conflicted with what has been scored in the matrix. For example, P3 of *Ascioplaga mimeta* (Neboiss) was indicated in the labelled figure (Fig. 5 in Hörnschemeyer, 2009), whereas this character was coded as absent in the data matrix (Hörnschemeyer, 2009). In addition, a new character, the presence or absence of a fixing epipleural fold at the elytral apex, was added.

Parsimony analyses were performed with the program TNT version 1.5 (Goloboff *et al.*, 2008) assigning equal and implied weights. In the implied weighting analysis, the concavity value (*K*) was set to 12, which has been proven to yield a better topology against homoplastic characters (Goloboff *et al.*, 2018). Most parameters were set as default in the "new technology search", while the value for "find min. length" was changed from 1 to 1000. For each analysis, a majority-rule consensus was calculated, and non-parametric bootstrap analysis

was implemented by 10,000 pseudoreplicates. Character states were mapped onto the trees with WinClada version 1.0 (Nixon, 2002). Trees were drawn with the online tool iTOL version 4.2.3 (Letunic & Bork, 2016) and graphically edited with Adobe Illustrator CC 2017.

Results

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Family Cupedidae Laporte, 1836 *sensu stricto*

Genus *Priacma* LeConte, 1861

†*Priacma megapuncta* Li & Cai sp.n. (Figs 2, 3, S4)

http://zoobank.org/urn:lsid:zoobank.org:act:3495A03B-EECE-4120-B5CF-73268DFB39AC.

Fig. 2. General habitus of *Priacma megapuncta* **sp.n.**, holotype, NIGP168831. A, dorsal view. B, ventral view. C, lateral view. Scale bars, 1 mm.

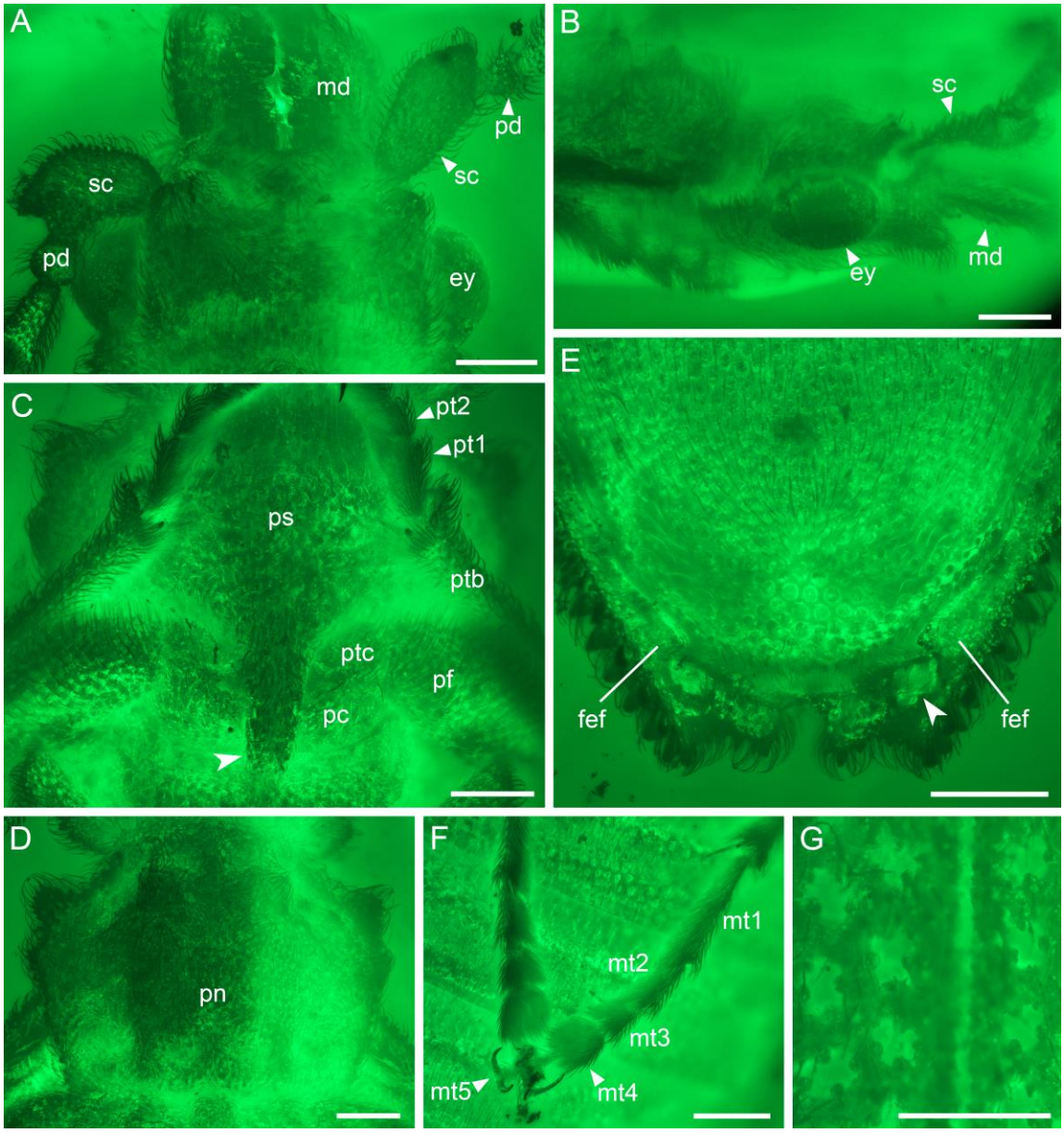

Fig. 3. Details of *Priacma megapuncta* **sp.n.**, holotype, NIGP168831, under epifluorescence. A, B, head. A, dorsal view. B, lateral view. C, D, prothroax. C, ventral view, showing the prosternal process extending beyond the posterior margin of conical procoxae (arrowhead). D, dorsal view. E. elytral apices in ventral view, showing the large window puncture (arrowhead) and fixing epipleural fold present at the elytral apices. F, metatarsi. G, maculated window punctures on the elytra. Abbreviations: ey, compound eye; fef, fixing epipleural fold; md, mandible; mt1–5, metatarsomeres 1–5; pc, procoxa; pd, pedicel; pf, profemur; pn, pronotum; ps, prosternum; pt1,2, protarsomeres 1,2; ptb; protibia; ptc, protrochanter; sc, scape. Scale bars, 400 μm.

Etymology. The specific epithet is a combination of the Latin "*mega*-" and "*puncta*", referring to the unusually large window puncture at the apex of each elytron.

Material. Holotype, NIGP168831. The fossil beetle is a well-preserved adult, with some body parts slightly polished away, including the apical antennomeres of the right antenna and the apex of the left mandible.

Locality and horizon. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, upper Albian or lower Cenomanian.

Diagnosis. The new species *P. megapuncta* can be separated from other *Priacma* species by the following combination of features: antennae slightly longer than half of the body length; pronotum with double tips at anterior corners; prosternal process extending beyond posterior margin of procoxae; and elytra with a single larger window puncture near elytral apex.

Description. Body elongate, 11.79 mm long, flattened, covered with short setae; scales absent; cuticle tuberculate. Head (Fig. S4A) subtriangular, 2.0 mm long (including mandibles) and 2.1 mm wide; dorsal protuberances (supraantennal and supraocular tubercles) on head inconspicuous, similar to that of *P. serrate*, inconspicuous. Compound eyes elliptical (not round as in *P. serrata* (LeConte)) from lateral view (Fig. 3B). Temples narrower than eyes, prominent. Antennae (Figs 3A; S4A, C) long, inserted laterally, reaching mid length of body, with 11 antennomeres, filiform; scape broad, flattened and curved, with serration on the edge; pedicel short; flagellomeres progressively becoming thinner distad with similar length, although apical antennomere slightly longer than others. Mandibles (Figs 3A; S4A, B) large and flattened; inner part of the dorsal surface blackened; inner margin also with wide and blunt teeth. Maxillary palpi reaching the mandible tip (Fig. S4B). Galeae capitate (Fig. S4B). Gular sutures not visible. Prementum reduced; ligula missing; mentum, submentum and head capsule fused. Pronotum (Fig. 3C) subtrapezoidal, 1.85 mm long and 2.36 mm wide, slightly wider than head but narrower than elytra combined, with double tips at anterior corners; anterior

tip subtriangular; posterior tip blunt; anterior margin convex medially, completely covering neck constriction from dorsal view; lateral margins serrated. Prosternal process extending beyond the posterior margin of conical procoxae (Figs 3D; S4D). Metacoxae large, subtriangular. Trochanters small. Femora stout; metafemora not extending beyond lateral edge of hind body. Tibiae thinner and longer than corresponding femora. Tarsi 5-segmented; tarsomere 4 distinctly bilobed; meso- and metatarsi (Fig. 3F) with elongated tarsomere 1; basal four tarsomeres with dense and dark setae ventrally, and tarsomere 5 with sparse setae. Claws simple. Elytra elongate, 7.95 mm long and each 1.51 mm wide, with ten rows of irregular and rounded window punctures with 4–5 maculae (Fig. 3G) as well as a single larger maculated window puncture near apex (Figs 3E; S4E, G); difference between primary veins and secondary veins inconspicuous; elytral apices emarginate (Figs 3E; S4E, G); notch extending beyond apex of abdomen; two rows of teeth well developed along distal five-sixths of lateral margins of elytra (Fig. S4F); fixing epipleural fold present at elytral apices (Figs 3E, S4G). Abdomen elongate, apex acute, rounded, with five visible ventrites; ventrite 5 twice as long as ventrite 4; all ventrites except the first markedly depressed anteriorly and overlapping the successors from below.

Remarks. The overall body shape of *P. megapuncta* **sp.n.** is superficially similar to that of extant *Paracupes* species from South America, but it differs from the latter by many significant features (see discussion below). The fossil can be assigned with confidence to the *Paracupes*-related genus *Priacma* as evidenced by the distinct subtruncate elytral apices, the peculiar rows of sharp teeth along the lateral elytral margins (also found in *Paracupes* and *Mesocupes admotus* (Ponomarenko); Kirejtshuk *et al*., 2016), and the presence of fixing epipleural folds near elytral apices (a synapomorphy of *Priacma*). All characters are distinctive among all extant cupedids, and they have been regarded as important diagnostic features for *Priacma* (Kirejtshuk *et al*., 2016). In addition, *P. megapuncta* has widely separated antennae (distance between antennal insertions more than half the distance between eyes), and elongate and robust mandibles. Both characters are supportive of such a placement, although they may also be interpreted as plesiomorphies of Cupedidae.

Phylogenetic assessment of Priacma megapuncta ***sp.n.***

Parsimony analyses using equal weights yielded 672 most parsimonious trees (280 steps long), in which Archostemata (excluding Jurodidae), Ommatidae and Cupedidae were all recovered as monophyletic groups, with moderate to strong support (Fig. S5). Micromalthidae and Crowsoniellidae were clustered together with relatively low support (bootstrap value = 52), and together were placed as the sister clade to the rest of Archostemata. The implied weighting analysis (K = 12) yielded three most parsimonious trees, and most clades supported under equal weights were also recovered, though Micromalthidae and Crowsoniellidae were placed as the sister group of Cupedidae (Fig. 4). Regarding the systematic position of the fossil species *P. megapuncta* **sp.n.**, both results under parsimony, using equal weights and implied weighting, indicated *P. megapuncta* as sister to *P. serrata* (bootstrap values = 27 and 42, respectively).

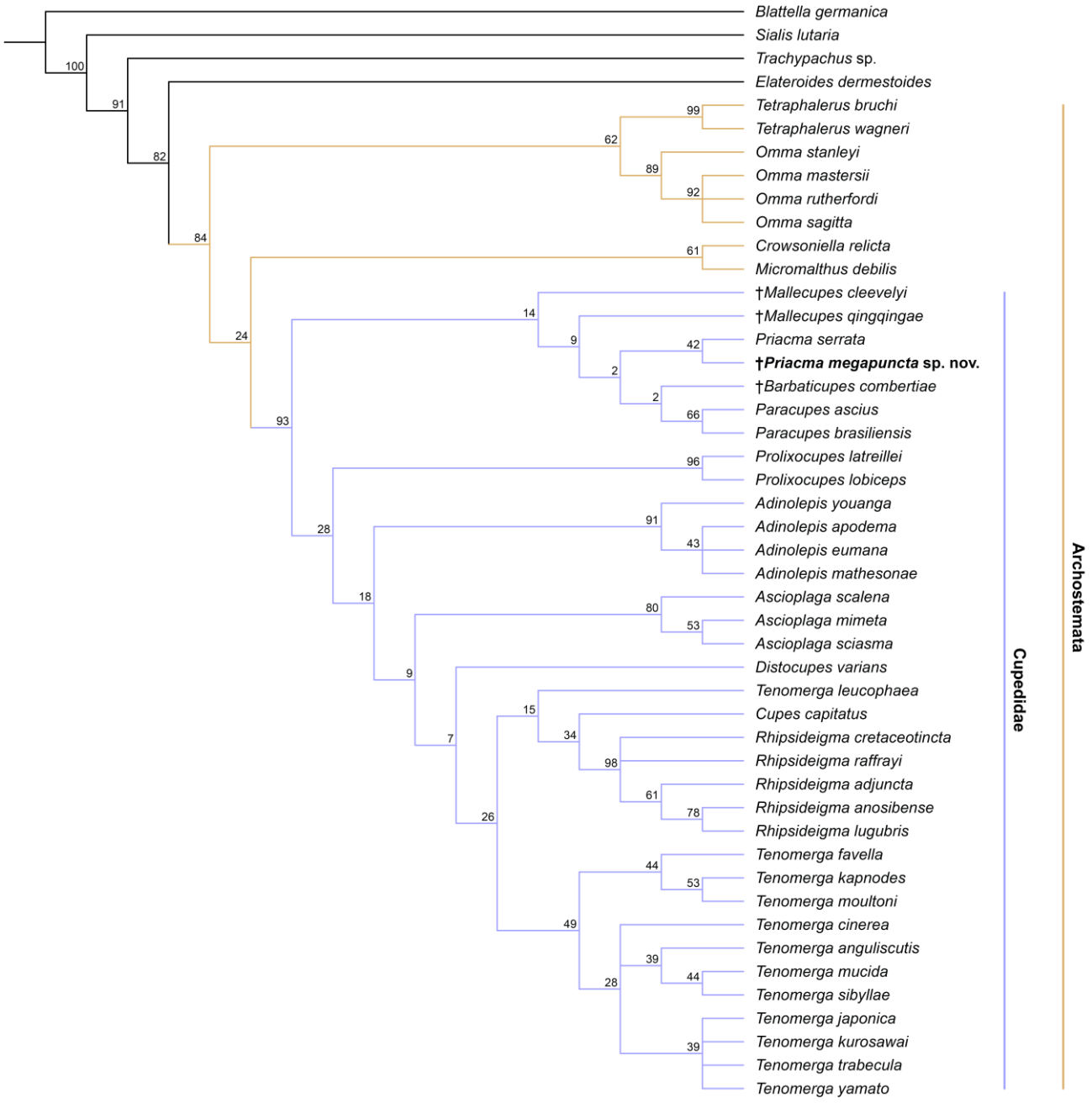

Fig. 4. Majority-rule consensus tree of three equally shortest trees (280 steps, CI = 0.62, RI = 0.83) from TNT implied weighting parsimony analysis.

Phylogeny of Cupedidae

In both parsimony analyses, the monophyly of Cupedidae was recovered with strong supporting values (Figs 4, S5). Similarly, a close relationship between *Priacma* and *Paracupes* was supported in both analyses, and the two extant genera, together with the Cretaceous *Barbaticupes* Jarzembowski *et al.*and *Mallecupes* Jarzembowski *et al.*, formed a sister clade to the rest of crown-group Cupedidae. Considering the extant taxa,

this result is consistent with that recovered in Hörnschemeyer (2009), but not in Beutel *et al.* (2008), in which they suggested *Priacma* as a sister group to the remaining genera. Among the 'derived group', *Prolixocupes* Neboiss was recovered in both analyses as sister to the remaining cupedid genera, including *Adinolepis* Neboiss, *Ascioplaga* Neboiss, *Cupes* Fabricius, *Distocupes* Neboiss, *Rhipsideigma* Neboiss and *Tenomerga* Neboiss. The relationships among *Adinolepis*, *Ascioplaga* and *Distocupes* were not well resolved, because the supporting values were generally very low. The clade including the genera *Cupes*, *Rhipsideigma* and *Tenomerga* was recovered in both analyses, although the *Tenomerga* is not monophyletic as found in Hörnschemeyer (2009). The peculiar species *T. leucophaea* (Newman), together with *Cupes* and *Rhipsideigma*, formed a clade. And this monophylum represented the sister group of the remaining species of *Tenomerga*.

Apomorphies of selected clades based on the implied weighting parsimony analysis are presented in Fig. S6. The monophyly of Cupedidae is supported by four apomorphic characters: tips of P1 blunt and rounded, blunt and conical, or acute and conical (ch. 10), anterior corners of pronotum not rounded (ch. 41), subapical tarsomere wider than apical tarsomere (ch. 46), and parameres with apical hooks (ch. 76). *Priacma*, *Paracupes* and the Cretaceous genera *Barbaticupes* and *Mallecupes* formed a monophyletic group as defined by a single non-homoplasious character: presence of large and elongated mandibles (ch. 24). A sister relationship between *P. megapuncta* **sp.n.** and *P. serrata* is supported by the obvious fixing epipleural fold at the elytral apex (ch. 57). The remaining cupedids, excluding *Priacma*, *Paracupes*, *Barbaticupes* and *Mallecupes*, are supported by dense, thick and inflated scales on the head (ch. 4), 3 to 4 basal antennomeres with special scales (ch. 21), ventral surface of mandible with at least two differently structured areas separated by a ridge or a groove (ch. 27), and the characteristic of the scales covering window punctures (ch. 50). Most supported groups in this clade are consistent with the result of Hörnschemeyer (2009). However, *Adinolepis* and *Ascioplaga* were not recovered as sister groups. The clade comprising *Ascioplaga*, *Distocupes*, *Cupes*, *Rhipsideigma*, and *Tenomerga* was supported by the shape of the anterior tip of protuberances P2 (ch. 12).

Phylogenetic relationships among archostematan families

As originally defined in Lawrence & Newton (1995), Archostemata includes four extant families: Cupedidae, Ommatidae, Micromalthidae, and Crowsoniellidae. The enigmatic Jurodidae is excluded in this study, because it seems to intermingle features belonging to Adephaga, Archostemata and Polyphaga (Yan *et al*., 2014). The

results under parsimony, using both equal weights and implied weighting, recovered the monophyly of Cupedidae and Ommatidae (Figs S5, 4). The monophyly of Ommatidae is moderately supported (bootstrap values = 62 and 62), whereas it is strongly supported for Cupedidae (bootstrap values = 95 and 93). A close relationship between Crowsoniellidae and Micromalthidae is supported in the parsimony analyses, but the bootstrap values are relatively low. The relationships among these four families are not well resolved.

Discussion

The extant genus *Priacma* has a sole species, *P. serrata*, confined to the west of the Rocky Mountains (North America), including California, Oregon, Washington, Idaho, Montana, and British Columbia (Kirejtshuk *et al*., 2016). Our discovery of a fossil species of *Priacma* from the mid-Cretaceous Burmese amber represents the first definite representative of this relict genus in the fossil record. The exceptional preservation of *P. megapuncta* **sp.n.** allows for a new interpretation of the evolution of morphological characters. In *P. serrata*, setae covering both dorsal and ventral sides are white and scale-like, making its cuticle invisible. However, the fossil species *P. megapuncta* does not have such scales, and setae are sparse. All extant cupedids and some ommatids have more or less scales, whereas *Crowsoniella* Pace (Crowsoniellidae) and *Micromalthus* LeConte (Micromalthidae) are glabrous (Hörnschemeyer *et al.*, 2002). Hörnschemeyer *et al.* (2002) suggested that the presence of scales in Ommatidae and Cupedidae is probably plesiomorphic, and *Crowsoniella* and *Micromalthus* secondarily lost them. However, given the absence of obvious scales in *P. megapuncta* and *Mallecupes cleevelyi* (Cupedidae), as well as *Brochocoleus zhiyuani* Liu *et al.*, 2017 and *Stegocoleus caii* Jarzembowski & Wang, 2016 (Ommatidae), it is more likely that the scales originated independently in both families. A recent molecular-based study indicated Ommatidae (*Tetraphalerus* Waterhouse) as a sister group to Micromalthidae (*Micromalthus*), and they together being sister to Cupedidae (McKenna *et al.*, 2015). This phylogenetic result also suggests that scales in Ommatidae and Cupedidae probably evolved independently.

In extant Cupedidae except for *P. serrata*, antennal insertions are narrowly separated by less than one diameter of the compound eye (or two diameters of the scapus; Hörnschemeyer, 2009; Hörnschemeyer & Yavorskaya, 2016). By contrast, the distance between antennal insertions of *P. serrata* and most other archostematan species are longer than the diameter of the eye (Hörnschemeyer, 2009; Hörnschemeyer & Yavorskaya, 2016). Similar to *P. serrata*, the distance is large in *P. megapuncta*, and fossil species *M. cleevelyi*

and *M. qingqingae* from the same amber locality also have widely separated antennal insertions, although the antennae of the third Burmite species, *Barbaticupes combertiae*, are relatively closer to each other. The antennae of *P. serrata* are distinctly short among cupedids, not reaching the mid length of the body (Bouchard, 2014), whereas in *P. megapuncta* and other cupedids the antennae are longer. The protuberances on the head are important features for generic-level identification of Cupedidae (Hörnschemeyer *et al*., 2006; Hörnschemeyer, 2009). Most cupedids bear conspicuous dorsal protuberances, but the protuberances in some cupedids such as *Priacma* and *Paracupes*, are relatively low. Our fossil species has inconspicuous supraantennal (P1) and supraocular (P2) protuberances on the head, suggesting it belongs to this group of Cupedidae. Indeed species of *Mallecupes* even possess no posterior protuberances. However, *B. combertiae*, which was recovered as the sister group of *Paracupes* in our analyses, has distinctive head protuberances, which may raise an important issue that head protuberances in different genera could be homoplasious. All extant archostematan species except *Crowsoniella* and *Micromalthus* possess a prementum (Hörnschemeyer, 2009). For example, the prementum in *P. serrata* is triangular with a ligula on it (Hörnschemeyer *et al*., 2002), but this structure is reduced in *P. megapuncta*, a feature unique among all known cupedids. In *Mallecupes*, the prementum and ligula are also not visible, however, due to the relatively poor preservation state and limits of observational methods; whether prementum and ligula are indeed reduced or not in *Mallecupes* still requires further study. There are two tips at the anterior corners of the pronotum in *P. megapuncta*, whereas only a single tip is developed in *P. serrata* (Hörnschemeyer, 2009). In *P. serrata*, the prosternal process is short, only reaching (or slightly extending beyond) the posterior margins of the procoxae (Hörnschemeyer, 2009). However, the prosternal process of *P. megapuncta* is comparatively long, obviously extending beyond the posterior margins of the procoxae, similar to *Paracupes* and many other derived cupedids. The length of the prosternal process may vary within the genus *Priacma*, but it may be considered as a diagnostic feature at a species level. We propose that this character cannot be taken as a diagnostic feature of *Priacma* as previously adopted by Tan *et al.* (2006a).

The most unusual character of *P. megapuncta* is the presence of a large window puncture near the apex of each elytron. To our knowledge, there is no such a modification of elytra in other extant or extinct cupedids. The well-developed fixing epipleural fold near the elytral apex in *P. serrata* is unique among extant cupedids (Kirejtshuk *et al*., 2016), so the close affinity of *P. serrata* to the fossil species *P. megapuncta* is strongly

supported by this potential synapomorphy of the genus. This is the first evidence indicating that the largely unnoticed fixing epipleural fold on the ventral side of the elytra can be fossilized in amber, although it has been suggested that it is not possible to trace this feature in fossils (Kirejtshuk *et al*., 2016). The exact function of the fixing epipleural folds remains elusive, but they may function in the fixation of the abdomen and elytra, which has been provisionally interpreted as an adaptation to aquatic or wet conditions (Kirejtshuk *et al*., 2016). Another intriguing feature of *P. megapuncta* is the toothed elytral margins. As in extant *P. serrata* and *Pa. brasiliensis* Kolbe, the elytral margin bears two stripes of sharp teeth, whereas such stripes are greatly reduced in *M. qingqingae* and *Pa. ascius* Neboiss, and absent in other derived cupedids (Kirejtshuk *et al.*, 2016).

Our phylogenetic analyses indicate that *Priacma* and *Paracupes*, as well as the Cretaceous genera *Barbaticupes* and *Mallecupes*, together represent an early branching clade of Cupedidae, which may be defined as a monophyletic tribe Priacmini. Hörnschemeyer & Yavorskaya (2016) suggested that *P. serrata* is the sister group to all other cupedid genera, but they did not provide any supporting evidence. It is probable that such a hypothesis was based on the results by Beutel *et al.* (2008), in which they focussed on the phylogeny of both extant and extinct families of Archostemata. Notably, in one of the analyses (with fossil taxa excluded) by Beutel *et al.* (2008), the relationships among *Priacma*, *Paracupes* and other genera are unresolved. Both *Priacma* and *Paracupes* are very small genera; *P. serrata* has a relatively wide distribution in western North America (Bouchard, 2014; Kirejtshuk *et al*., 2016), while the two extant species of *Paracupes* are restricted to South America: *Pa. brasiliensis* from eastern Brazil, and *Pa. ascius* from Ecuador (Neboiss, 1989; Hörnschemeyer & Yavorskaya, 2016). Our discovery of a new fossil species belonging to extant *Priacma* has important biogeographic implications (Fig. 5). It indicates that *Priacma* also occurred in the ancient tropical forest where later became today's southeastern Asia, with a likely subsequent move into North America where the extant member of the genus is now found. Recent molecular dating analyses indicated that stem-group Cupedidae originated in the Late Jurassic, approximately 157.82 million years ago (McKenna *et al*., 2015). By contrast, another molecular dating of beetles by Zhang *et al*. (2018) suggested an Early Triassic age for the origin of Cupedidae. The former result conflicts with the fossil record of Cupedidae, because diverse cupedids have been reported from the Middle Jurassic Daohugou beds (ca. 165 Ma) in northeastern China (Tan *et al.*, 2006b, 2007; Tan & Ren, 2009; Kirejtshuk *et al*., 2016). Therefore, it is appropriate to suggest that Cupedidae probably had a much longer history, at least as far back as the Middle

Jurassic, which is more consistent with the hypothesis by Zhang *et al*. (2018). Unfortunately, the precise systematic positions of the Jurassic cupedids from Daohugou have never been tested in a phylogenetic context. Indeed, many key features can be extracted from those fossils: they have widely separated antennae as in *Priacma*, but unlike *Priacma* and *Paracupes*, they have small mandibles and smooth (non-toothed) elytral margins (Tan *et al*., 2006b, 2007) as found in more derived extant cupedids (Hörnschemeyer, 2009). As such, the relationship between the Jurassic fossils and extant cupedids remains a mystery. New discoveries of phylogenetically-informative cupedids from Cretaceous ambers (e.g., mid-Cretaceous Burmese amber, Early Cretaceous Spanish amber and Lebanese amber) and other exceptional faunas will hopefully help to reconstruct the evolutionary dynamics of this archaic family, which has likely suffered from severe extinction events during its long geological history.

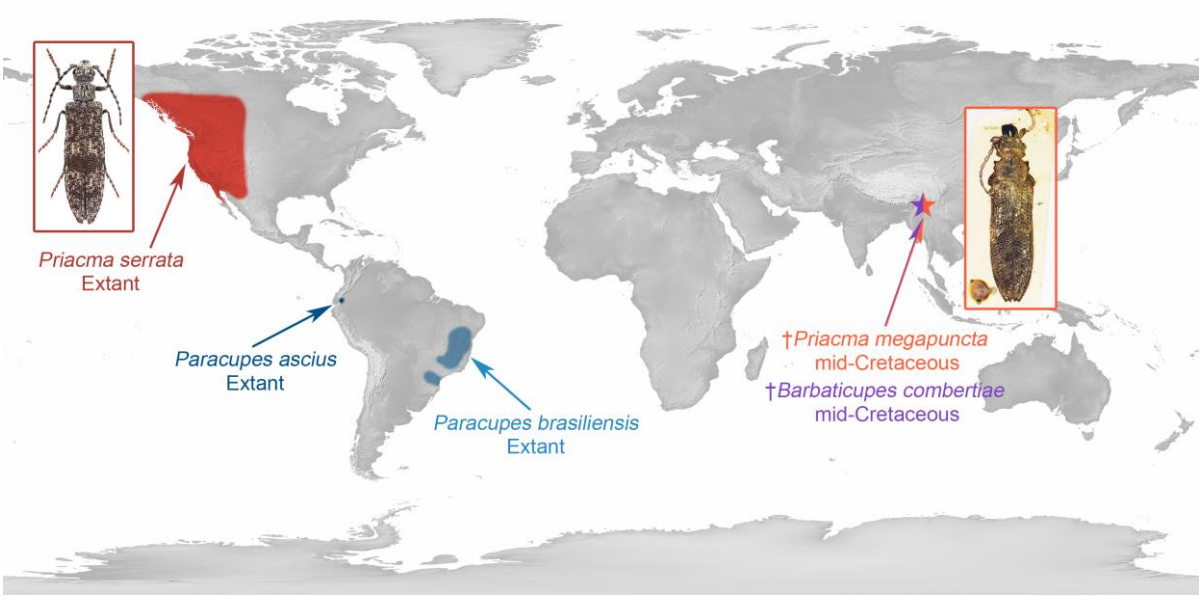

Fig. 5. Geographic distribution of several basal cupedid genera: *Priacma*, *Paracupes* and *Barbaticupes*. World map was made with Natural Earth (NaturalEarthData.com).

The monophyly of the suborder Archostemata is strongly supported by our phylogenetic results, and by many other works based on both morphological (e.g., Beutel *et al*., 2008; Hörnschemeyer *et al*., 2006; Hörnschemeyer, 2009; Lawrence *et al*., 2011) and molecular data (Bocak *et al*., 2014; McKenna *et al*., 2015; Kusy *et al*., 2018; Linard *et al*., 2018). However, the relationships among all extant archostematan families remain elusive. The phylogenies based on morphological characters (both larval and adult) are unable to

356 confidently resolve the relationships among extant archostematan families. In particular, as shown in
357 Hörnschemeyer (2009), different phylogenetic methodologies using parsimony and Bayesian inference yield
358 slightly conflicting topologies in deeper nodes. When the fossil species were added, the relationships among
359 Cupedidae were not well resolved as well. Lawrence *et al*. (2011) provided a phylogenetic tree of Coleoptera
360 based on 516 adult and larval characters. According to their result under implied weighting parsimony, both
361 Cupedidae and Ommatidae were recovered as polyphyly. However, our Bayesian analysis (using the discrete
362 Marcov k model) of the same dataset strongly supported the monophyly of the two families (Cai, unpublished
363 result). The molecular-based phylogenetic studies are promising for elucidating the interrelationships in
364 Archostemata, but published results appear limited by insufficient taxon and gene sampling, and the effects of
365 missing data (Bocak *et al*., 2014; McKenna *et al*., 2015; Kusy *et al*., 2018; Linard *et al.*, 2018). One of the
366 challenges we are facing is that *Crowsoniella relicta* Pace (Crowsoniellidae) has not been sequenced because
367 so far only three specimens are known. Despite the uncertainties in both morphology and molecular based
368 phylogenetic studies of Archostemata, the monophyly of Cupedidae is well supported by almost all published
369 trees (e.g., Beutel *et al*., 2008; Hörnschemeyer, 2009; McKenna *et al*., 2015) except the one by Lawrence *et al*.
370 (2011). A re-discovery of new material of *C. relicta* (and the puzzling *Sikhotealinia zhiltzovae*) and further
371 DNA-based phylogenetic studies will be of great significance of reconstructing the backbone phylogeny of the
372 suborder Archostemata.
373
374 **Conclusions**
375 Our discovery of a new species belonging to Cupedidae from the mid-Cretaceous Burmese amber represents
376 the fourth record of the family in this fossil locality. It highlights the palaeodiversity and morphological
377 disparity of Cupedidae in the late Mesozoic. Phylogenetic analyses demonstrated that *Priacma megapuncta*
378 **sp.n.** is a sister group to the extant peculiar species *P. serrata* from North America, indicating that *Priacma* is
379 an ancient genus and was once much more widespread in the Cretaceous. Many interesting features of *P.*
380 *megapuncta*, including large mandibles, toothed elytral margins, and elytral apices with fixing epipleural folds,
381 are important for understanding the early evolution of Cupedidae. Further discoveries of fossil cupedids from
382 Mesozoic exceptional faunas, as well as robust molecular-based phylogenies based on a more extensive
383 sampling of extant taxa and molecular markers, will contribute to elucidating the long evolutionary history of

Cupedidae.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Details of *Barbaticupes combertiae*, under epifluorescence. A, B, D, NIGP166315. A, head and prothroax in dorsolateral view. B, head in ventrolateral view, showing the gula. D, distal part of right elytron, dorsolateral view, showing the elytral scales confined to primary veins. C, NIGP166314, aedeagus in ventral view. Abbreviations: ah, apical hook; ey, compound eye; p1,2, supraantennal and supraocular protuberances, respectively; gu, gula; mxp, maxillary palpi; pm, paramere; sc, scape; v5, ventrite 5. Scale bars: 400 μm in A; 200 μm in B–D.

Fig. S2. Details of *Mallecupes qingqingae*, under epifluorescence. A, C, D, NIGP157008. A, head and prothroax in ventrolateral view. C, distal parts of elytra, ventrolateral view. D, middle part of right elytron, lateral view, showing the outermost row of large maculated window punctures. B, NIGP164791, maculated window punctures on the elytra. Abbreviations: ey, compound eye; gu, gula; md, mandible; ps, prosternum; sc, scape. Scale bars: 400 μm in A, C; 200 μm in B, D.

Fig. S3. Details of *Mallecupes cleevelyi*, NIGP164792, under epifluorescence. A, head in ventral view. B, prothroax in ventral view, showing the prosternal process not extending beyond the posterior margin of conical procoxae (arrowhead). C, maculated window punctures on the elytra. D, distal parts of abdomen and left elytron, ventral view. Abbreviations: ey, compound eye; fl1, flagellomere 1; md, mandible; mxp, maxillary palpi; pc, procoxa; pd, pedicel; pf, profemur; ps, prosternum; sc, scape; v5, ventrite 5.Scale bars: 200 μm.

Fig. S4. Details of *Priacma megapuncta* **sp.n.**, holotype, NIGP168831, under incident light. A, B, head. A, dorsal view. B, ventral view, showing the mouthparts. C, proximal portion of the left antenna. D, prothroax in

ventral view, showing the prosternal process extending beyond the posterior margin of conical procoxae (arrowhead). E–G, distal parts of elytra. E, G, dorsal and ventral, respectively, showing emarginate elytral apices and the large window punctures. F, lateral view, showing the double stripes of teeth. Abbreviations: fl1,2, flagellomeres 1,2; gl, galeae; lbp, labial palpi; mxp, maxillary palpi; pd, pedicel; sc, scape. Scale bars: 500 μm in A–E, G; 1 mm in F.

Fig. S5. Majority-rule consensus tree of 672 equally shortest trees (280 steps, CI = 0.62, RI = 0.83) from equally weighted parsimony analysis using TNT.

Fig. S6. Majority-rule consensus tree from implied weighting parsimony analysis, with character state labeled. A, Archostemata. B, Cupedini. Black circles indicate non-homoplasious changes; white circles indicate homoplasious characters; numbers above the branches of the strict consensus tree indicate character numbers.

File S1. List of characters used in the phylogenetic analyses.

File S2. Morphological dataset (47 taxa and 110 morphological characters) used for the analyses.

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